FOLIAR TRICHOMES OF QUERCUS SUBGENUS QUERCUS IN THE EASTERN UNITED STATES

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SINCE DYAL'S PUBLICATION of a key to the oaks of the eastern United States (1936), an increasing amount of attention has been paid to the trichomes that collectively contribute to foliar pubescence. Her characterization of oak trichomes included two basic types, glandular and nonglandular, and some quantitative data regarding size (the tip-to-tip extent of the rays, which she called the spread). The information was integrated with that for other vegetative features to produce a workable key to the species of *Quercus* L. as they were then understood. Trichomes have also been used as evidence to detect hybridization among species of white oaks (Tucker & Muller, 1958; Tucker, 1963; Maze, 1968; and others). These workers found that the number of ray branches and their spread conformed to the ranges of variability that could be associated with particular species. Hybridization between individuals of different species resulted in modification of these characters in a manner similar to other quantifiable characters also studied.

Because of the utility of evidence from trichome characters demonstrated by previous investigators, the present study was initiated to determine if quantifiable characters of the trichomes could be combined with the types to produce a valid set of characters for recognizing individuals of eastern white oak species. Furthermore, if the character sets proved to be uniform for the species, they could provide a basis for recognizing hybrids between them.

Most recently, trichome structure has been closely inspected by Hardin (1976), who defined ten types. Four of these fall into Dyal's glandular class, and the remaining six belong to her nonglandular group. In the glandular class, simple-uniseriate and bulbous types were found on leaves of the white oaks described here, but rosulate and simple-branched hairs were not observed. Examples of the simple-uniseriate and bulbous trichomes are pictured in FIGURES 5 and 12, respectively. Solitary (FIGURES 7, 16), fasciculate (FIGURES 2, 17), stipitate-fasciculate (FIGURES 10, 11), stellate (FIGURES 5, 15), and fused-stellate (FIGURES 12, 18) trichomes are nonglandular types that also occur. Multiradiate and appressed-lateral, nonglandular trichomes were not observed. Although Hardin's terms are more precise than Dyal's, hers are retained for convenience in referring to a trichome class in the descriptions that follow.

MATERIALS AND METHODS

Specimens for this study were obtained from herbaria of the Missouri Botanical Garden and Southern Illinois University, and from collections

by one of us (Thomson) from nine states over the past four years. In all, approximately 2000 specimens were utilized. From these, 50 were chosen from each species for assessment of trichome types and for obtaining the quantitative data, i.e., number of rays and ray spread. Specimens were selected to insure the broadest possible representation of the known extent of range and habitats of the species. These selected specimens served as the basis upon which characterization was established.

Trichomes were viewed with a light microscope at 100× using reflected light. All measurements were taken from trichomes occurring on the abaxial surface of leaves midway between base and apex and midvein and margin, and were done with an eyepiece micrometer. In an effort to avoid unwittingly choosing certain types over others, counts were made for those nearest the ten numbers of the ocular micrometer when superimposed. If more than one type was encountered, measurements were taken for ten of each. Range and mean were determined for number of rays per trichome and for spread (in mm.) for 500 trichomes of each species. A range for means of trichomes of individual leaves ($\overline{X}$ range) was also calculated for the two characters. Measurements were not made for glandular hairs.

All remaining specimens were viewed, and counts and measurements from three trichomes for each were compared to range and mean values established in the initial survey. Thus, the number of trichomes contributing to the establishment of the descriptive statistics varied from 500 for *Quercus alba* to 833 for *Q. macrocarpa* (50 specimens multiplied by 10 trichomes plus 111 additional specimens multiplied by 3 trichomes). One exception to this was *Q. oglethorpensis*, for which only ten specimens were available. However, because the species has a very limited distribution (Duncan, 1950), the values obtained are considered at least as representative of that taxon as were the 161 specimens of the comparatively far-ranging *Q. macrocarpa*. A summary of quantitative data for nonglandular trichomes by species is presented in TABLE 1. Values are not given for the solitary type hair since, by definition, it has only a single axis and no spread.

Scanning electron micrographs were prepared to show trichomes that are believed, from these data, to be representative of the species. Tissues were cut from leaves with a cork borer and fixed in cold (4°C) 3 percent glutaraldehyde in veronal buffer (pH 7.4) for two hours. After fixing, the tissues were washed twice with buffer for 15 minutes at 4°C and then fixed in 1 percent aqueous osmium tetroxide at 4°C for 30 minutes. Specimens were serially dehydrated in ethyl alcohol, further dehydrated in freon, critical point dried, and vacuum evaporated with carbon.

Species included in this study were: *Quercus alba, Q. austrina, Q. bicolor, Q. chapmanii, Q. durandii, Q. geminata, Q. lyrata, Q. macrocarpa, Q. margaretta, Q. minima, Q. montana* (*Q. prinus* auct., non Linnaeus), *Q. oglethorpensis, Q. prinoides* Willdenow, including var. *prinoides* and var. *acuminata* (*Q. muehlenbergii*), *Q. prinus* (*Q. michauxii* of some authors), *Q. stellata*, and *Q. virginiana*.

TABLE 1. Range, mean, and mean range for quantitative features of nonglandular trichomes of the eastern white oaks.

Species	Types	Spread (mm.)			Number of rays		
		Range	$\bar{X}$	$\bar{X}$ Range	Range	$\bar{X}$	$\bar{X}$ Range
Quercus alba	solitary						
	fasciculate	0.17-0.24	0.22	0.17-0.26	3- 8	5.1	4.5- 6.7
austrina	solitary						
	fasciculate	0.20-0.50	0.31	0.21-0.39	2- 9	5.0	4.2- 6.2
bicolor	fasciculate	0.30-0.65	0.53	0.36-0.55	2- 8	4.2	3.5- 5.1
	stellate	0.07-0.22	0.15	0.09-0.18	6-16	10.0	5.6-13.2
chapmanii	fasciculate	0.10-0.25	0.18	0.13-0.23	4- 9	6.8	5.1- 7.5
durandii	fasciculate	0.15-0.35	0.23	0.19-0.28	4- 9	6.5	4.9- 8.3
	stellate	0.10-0.20	0.14	0.11-0.18	8-16	12.6	7.3-13.6
geminata	stipitate, fused-stellate	0.20-0.45	0.29	0.24-0.33	7-17	11.1	8.6-13.7
	fused-stellate	0.14-0.21	0.15	0.12-0.19	8-14	11.5	11.0-16.5
lyrata f. *viridis*	solitary						
	fasciculate	0.10-0.30	0.20	0.11-0.19	2- 4	2.5	1.0- 3.0

f. lyrata	solitary						
	fasciculate	0.10-0.33	0.21	0.16-0.28	2- 6	3.4	2.8- 4.0
	stellate	0.10-0.22	0.12	0.09-0.24	6-16	10.1	6.5-12.2
macrocarpa	fasciculate	0.20-0.60	0.33	0.26-0.50	2- 9	4.6	3.4- 5.1
	stellate	0.10-0.26	0.14	0.12-0.25	4-16	7.8	6.2-10.6
margaretta	stipitate-fasciculate	0.40-1.00	0.64	0.40-0.77	4- 9	6.7	5.2- 8.2
minima	sessile, fused-stellate	0.07-0.19	0.12	0.10-0.15	7-17	12.6	7.5-17.8
montana	stipitate-fasciculate	0.10-0.25	0.14	0.16-0.29	2- 5	3.1	2.8- 4.3
	fasciculate	0.08-0.25	0.16	0.11-0.30	1- 5	2.4	1.9- 2.7
oglethorpensis	stipitate-fasciculate	0.20-0.40	0.32	0.25-0.37	3- 9	6.3	4.5- 7.9
prinoides							
var. prinoides	stellate	0.09-0.22	0.15	0.09-0.20	6-16	10.2	8.0-13.0
var. acuminata	stellate	0.09-0.22	0.15	0.11-0.21	6-16	9.2	7.1-12.0
prinus	solitary						
	fasciculate	0.20-0.45	0.33	0.22-0.39	2- 8	3.4	2.0- 4.9
stellata	fasciculate	0.15-0.49	0.31	0.20-0.39	4- 9	6.6	4.0- 8.7
virginiana							
var. virginiana	sessile, fused-stellate	0.06-0.18	0.11	0.09-0.16	9-18	15.6	13.6-16.5
var. fusiformis	sessile, fused-stellate	0.08-0.16	0.12	0.09-0.17	12-24	17.1	14.2-18.3

FOLIAR TRICHOMES OF THE EASTERN WHITE OAKS

Quercus alba Linnaeus

The leaves of white oak have usually been described as glabrous. In this study, however, three types of trichomes were observed. On the leaf surface minute, appressed, glandular hairs occur. These are typical for *Quercus alba*. Solitary, nonglandular hairs are occasionally found on the midvein. These may be associated with a yellowish, fasciculate hair occurring near the midvein, especially in vein axils. The trichomes do not always occur together. Most specimens had glandular hairs only, but some had both these and the nonglandular trichomes.

Fasciculate hairs of white oak have ray branches appearing twisted and flattened and are attached to epidermal cells that are slightly elevated from the surface, forming a pedestal. The rays extend an average of 0.22 mm. (range 0.17–0.24 mm.) and are 3 to 8 ($\overline{X}$ = 5.1) per trichome. Fasciculate hairs are numerous on young leaves but are shed as the leaf matures. Approximately 15 percent of the specimens of this study retained the hairs in the midvein area. The dehydrated appearance of the rays is presumably due to the fact that the cell walls are thinner than those of fasciculate hairs of the other eastern oaks that possess them (FIGURE 1). Solitary hairs vary from 0.14 to 0.29 mm. in length.

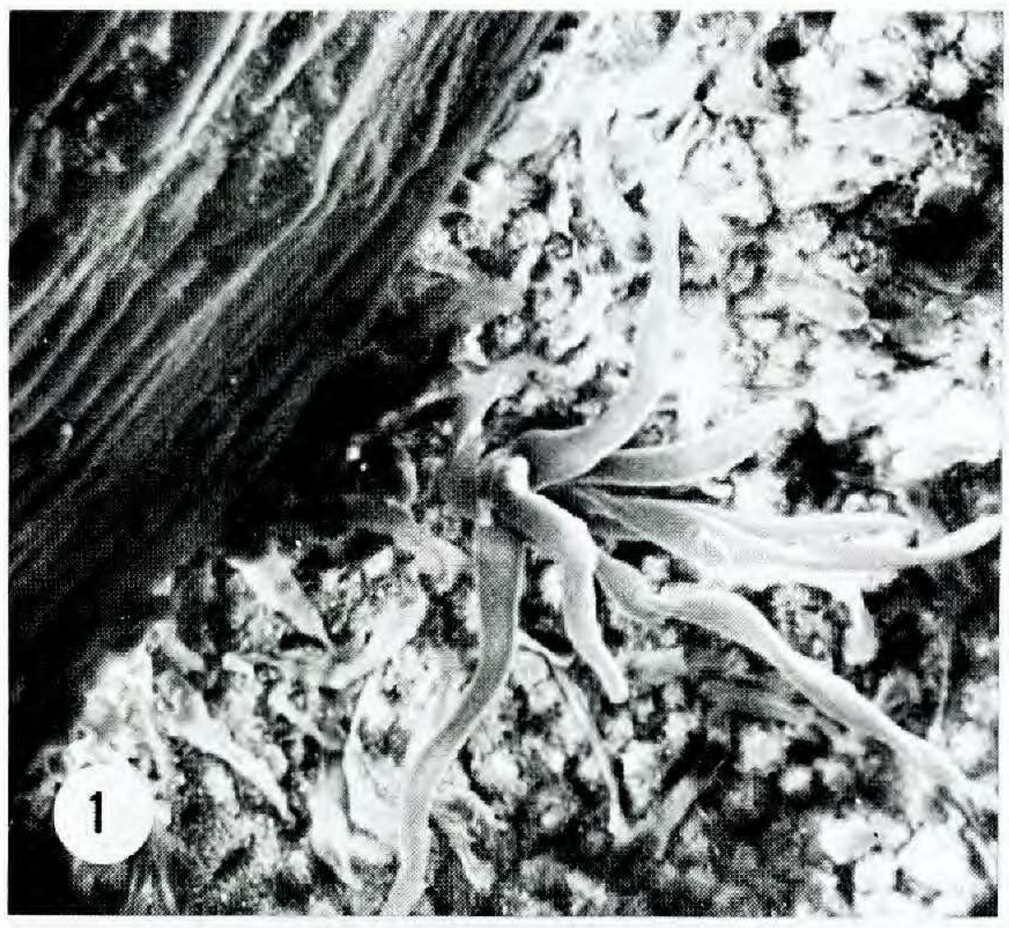
Quercus austrina Small

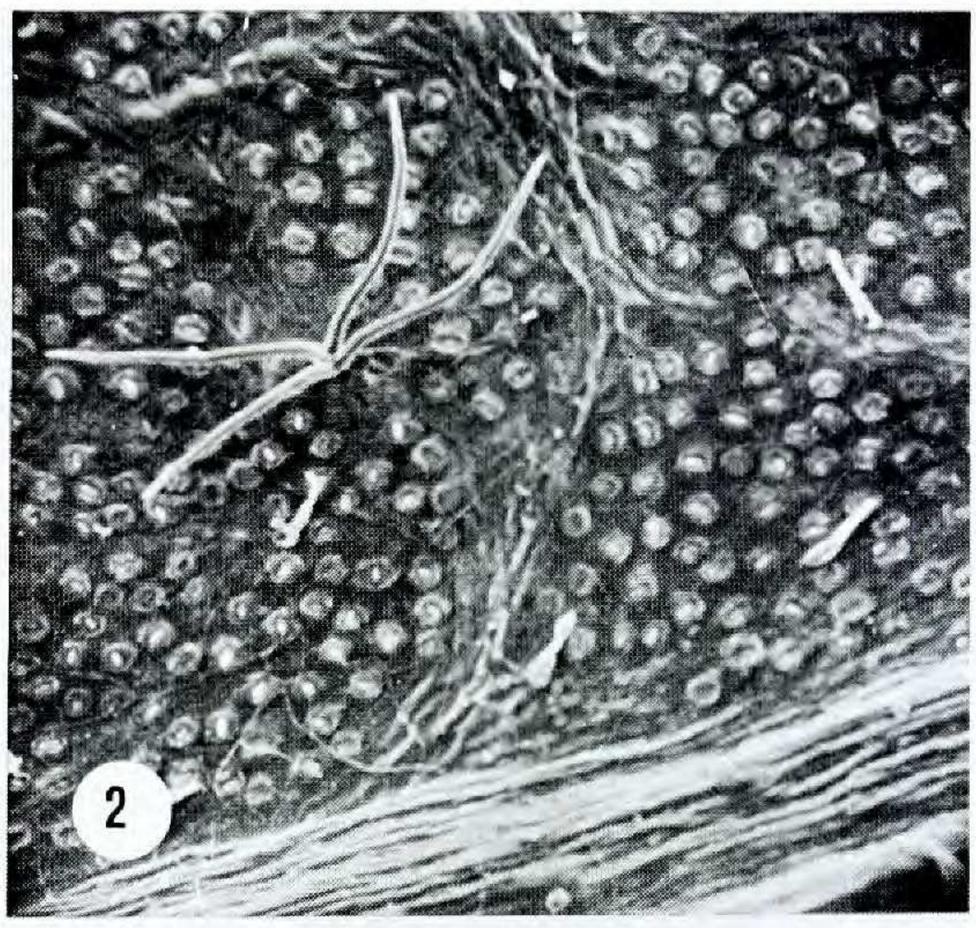
Nonglandular trichomes of bluff oak are restricted to the midvein area and are of both solitary and fasciculate types. Solitary hairs are more frequent than fasciculate trichomes, but both are fairly infrequent. Occurring on or near the midvein, the fasciculate type is pedestaled and yellow; it has a spread of 0.20–0.50 mm. ($\overline{X}$ = 0.31 mm.) and 2 to 9 rays ($\overline{X}$ = 5.0 rays). Solitary hairs vary from 0.20 to 0.40 mm. in length ($\overline{X}$ = 0.29 mm.) and are restricted to the midvein. Glandular hairs occur on the leaf surface between the principal veins and are simple-uniseriate, appressed, one- to three-celled, and yellowish. In their distribution, their types, and their size, the trichomes (FIGURE 2) are generally most similar to those of *Quercus alba*.

Quercus bicolor Willdenow

Swamp white oak possesses one of the most characteristic combinations of glandular and nonglandular trichomes among the white oaks. Nonglandular hairs are fasciculate and stellate. The fasciculate hairs are erect with 2 to 8 rays ($\overline{X}$ = 4.2) and a spread of 0.30–0.65 mm. ($\overline{X}$ = 0.53 mm.); they occur uniformly over the leaf surface. The stellate trichomes are appressed or looser with 6 to 16 rays ($\overline{X}$ = 10.0) and have a spread of 0.07–0.22 mm. ($\overline{X}$ = 0.15 mm.). Both of these types are whitened, but among them are erect, bulbous, glandular hairs that are red. These tend to become dark brown in pressed specimens (FIGURE 3).

Most specimens are quite densely pubescent, but *Quercus bicolor* var.





FIGURES 1–6: 1, *Quercus alba*, fasciculate hair, × 400; 2, *Q. austrina*, fasciculate hair, × 135; 3, *Q. bicolor*, fasciculate and stellate hairs, × 200; 4, *Q. chapmanii*, fasciculate hair, × 270; 5, *Q. durandii*, fasciculate and stellate hairs, × 135; 6, *Q. geminata*, stipitate, fused-stellate and sessile, fused-stellate hairs, × 200.

mollis Nutt., a variety with green leaves, has been described. In the few specimens of that taxon studied, no difference in trichome types was observed, although density of all was reduced.

Quercus chapmanii Sargent

Both glandular and nonglandular trichomes are present on the leaves of Chapman's oak. Simple-uniseriate, glandular hairs are minute, appressed, and yellow, and occur on the surface between principal veins. Often these are dense enough to color the leaf. The nonglandular trichome is considered fasciculate, although the rays tend to diverge in roughly the same plane. Pedestaled and yellow, it occurs on or near the midvein and primary veins. Rays vary from 4 to 9 ($\overline{X}$ = 6.8) and have a spread of 0.10–0.25 mm. ($\overline{X}$ = 0.18 mm.) (FIGURE 4).

Quercus durandii Buckley

Two sizes of nonglandular hairs occur on leaves of Durand's oak. The larger type is like that found on *Quercus austrina*. It is fasciculate, pedestaled, and yellow and occurs on or near the midvein and principal veins. Rays vary from 4 to 9 ($\overline{X}$ = 6.5) and measure 0.15–0.35 mm. ($\overline{X}$ = 0.23 mm.) across. The smaller type is stellate and measures 0.10–0.20 mm. ($\overline{X}$ = 0.14 mm.), but is more branched (8 to 16 rays averaging 12.6 branches per hair). Whitened and appressed, these occur on the leaf surface. FIGURE 5 shows both types.

Quercus geminata Small

This oak has been treated both as a variety of *Quercus virginiana* (var. *maritima* (Michaux) Sargent) and as a separate species. Its status is not something that this study intends to resolve; however, the trichome structure seems to us to differ sufficiently from that of *Q. virginiana* to warrant distinction.

Two sizes of nonglandular, fused-stellate hairs are present on leaves of *Quercus geminata* (FIGURE 6). The larger size occurs on the principal and lesser veins. Beyond the area of fusion, the rays are free and range from 7 to 17 per hair ($\overline{X}$ = 11.1) with a spread of 0.20–0.45 mm. ($\overline{X}$ = 0.29 mm.). The hairs are yellow or occasionally red in their centers. Beneath the larger hairs are smaller ones, 0.14–0.21 mm. ($\overline{X}$ = 0.15 mm.) across, which are appressed or slightly ascending. The hairs have 8 to 14 rays ($\overline{X}$ = 11.5) and are fused only near the base. Both sizes of trichomes are whitened in appearance.

The differences in trichomes for *Quercus geminata* and *Q. virginiana* are of an order typically seen only between distinct species.

Quercus lyrata Walter

With respect to trichome structure two leaf forms are known for overcup oak. One is a low-density form in which the leaf appears green to the unaided eye (f. *viridis* Trelease). Trichomes are nonglandular, erect, and either solitary or fasciculate and 2- to 4-rayed. Approximately half of the

specimens were observed to have a combination of solitary and 2-rayed hairs, while the remainder possessed these and 3- and 4-rayed forms. Overall, trichomes have 1 to 4 rays ($\overline{X} = 1.5$), with fasciculate hairs (2 to 4 rays) spreading 0.10–0.30 mm. ($\overline{X} = 0.20$ mm.). The hairs are distributed along the midvein and primary veins but occasionally arise from veinlets (FIGURE 7).

The second form (f. *lyrata*) is densely pubescent with two sizes of nonglandular hairs. The larger are solitary or fasciculate, yellow, and 2- to 6-rayed ($\overline{X} = 3.4$), with a spread of 0.10–0.33 mm. ($\overline{X} = 0.21$). The smaller are stellate, whitened, appressed or looser, with (4 to) 6 to 16 rays ($\overline{X} = 10.1$) that extend 0.10–0.22 mm. ($\overline{X} = 0.12$ mm.) (FIGURE 8). Trichomes of the dense form resemble those of *Quercus macrocarpa* in general appearance, but differ from them quantitatively (TABLE 1).

Quercus macrocarpa Michaux

Burr oak has nonglandular trichomes of two distinct size ranges. The larger are fasciculate with a spread of 0.20–0.60 mm. ($\overline{X} = 0.33$ mm.) and possess 2 to 9 rays, averaging 4.6 per trichome. Beneath these are smaller, stellate hairs measuring 0.10–0.26 mm. ($\overline{X} = 0.14$ mm.) across and having 4 to 16 rays, which average 7.8 per trichome. These are whitened and may be appressed or looser. Occasionally the nonglandular hairs are associated with simple-uniseriate, glandular, yellow ones (FIGURE 9).

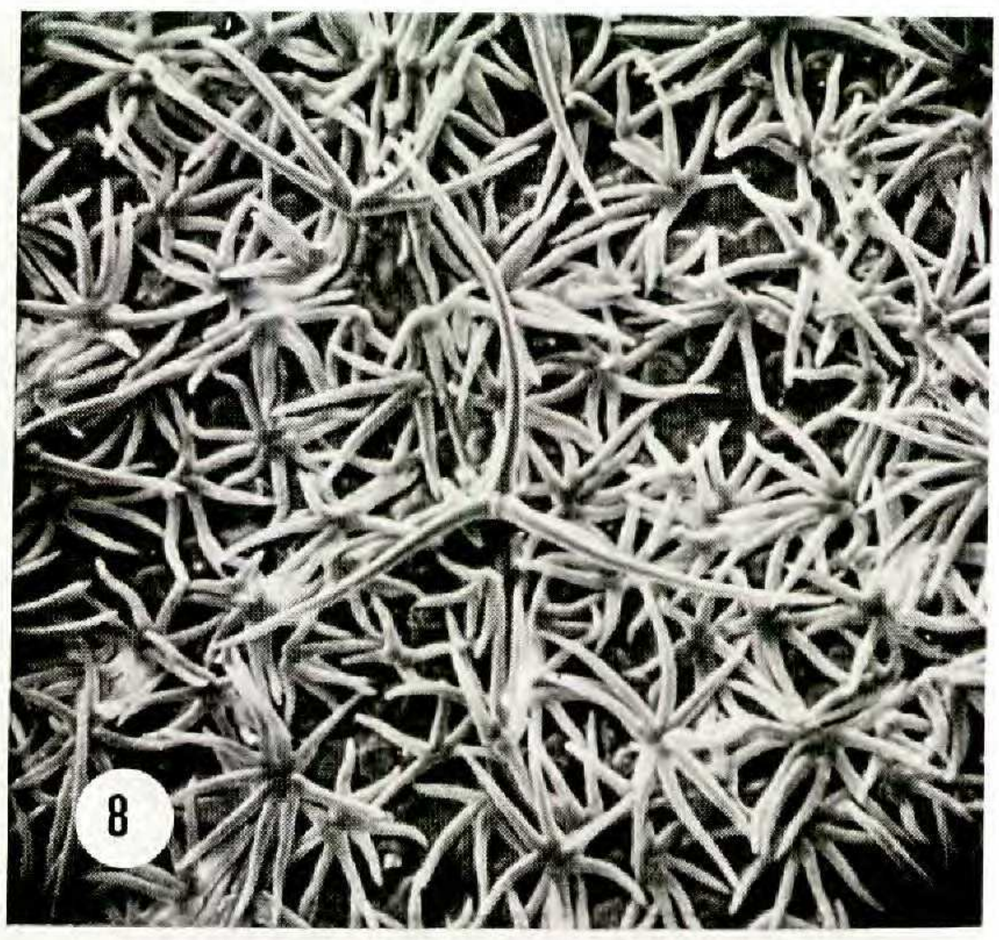
On approximately 10 percent of the specimens, only the larger trichomes are found. In such cases they are typically longer and have a greater spread than when they occur with the smaller form. We have no data from field studies with which to correlate this form to determine if it has ecological significance.

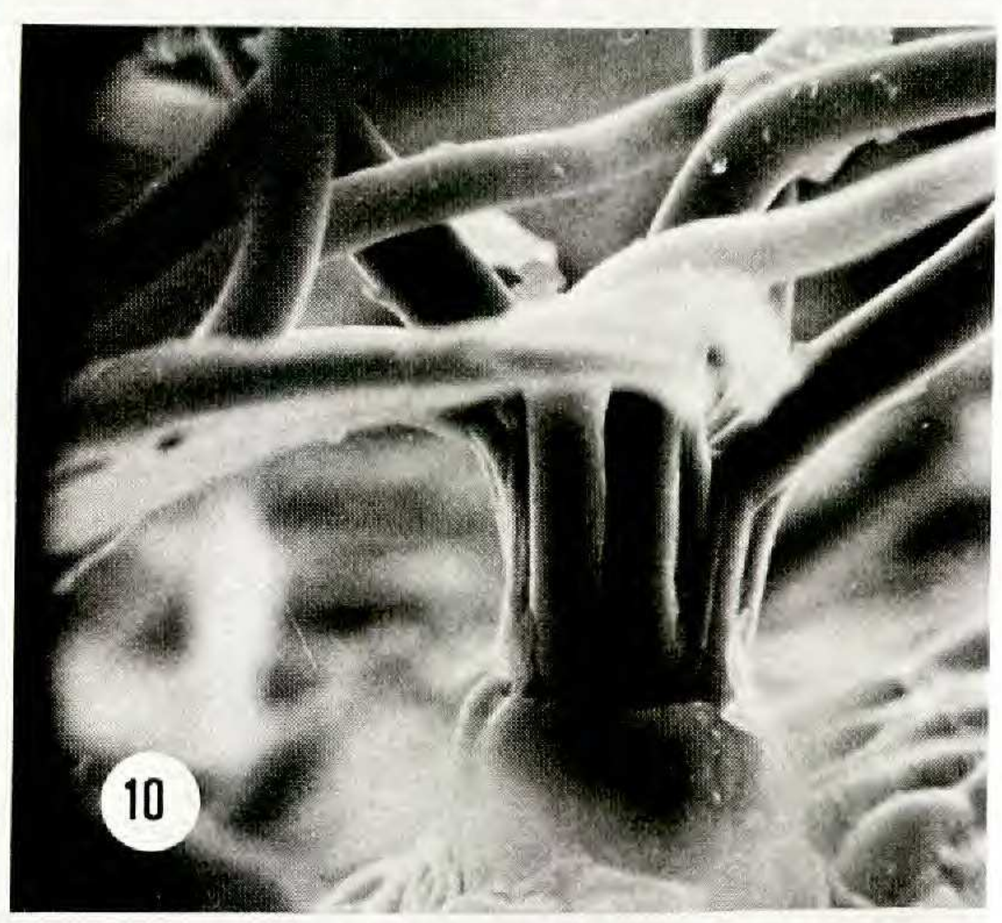
Quercus margaretta Ashe

In leaf form *Quercus margaretta* most closely resembles *Q. stellata*, but in trichome morphology the resemblance to *Q. oglethorpensis* is striking. As with Oglethorpe oak, the stipitate-fasciculate hairs arise from distinct pedestals, but they differ in size. Trichomes of *Q. margaretta* have the greatest spread of any of those of the eastern white oaks, 0.40–1.0 mm. ($\overline{X} = 0.64$ mm.). Rays range from 4 to 9 per hair and average 6.7. FIGURE 10 shows the pedestal at the base of the hair, while FIGURE 11 shows the entire hair. These are whitened or sometimes have a yellowish tint and are distributed upon veins. Simple-uniseriate hairs are also found on the leaves.

Quercus minima (Sargent) Small

Quercus minima is considered a variety of *Q. virginiana* by some taxonomists, and a distinct species by others. Little support is given the latter consideration by trichome structure, which is identical with that of *Q. virginiana*. The fused-stellate trichomes do, however, differ from those of *Q. virginiana* in number of rays and spread. Branches vary in number from





FIGURES 7–12: 7, *Quercus lyrata* f. *viridis*, solitary and fasciculate hairs, × 150; 8, *Q. lyrata* f. *lyrata*, fasciculate and stellate hairs, × 200; 9, *Q. macrocarpa*, fasciculate and stellate hairs, × 200; 10, *Q. margaretta*, stipitate-fasciculate hair showing stipe and pedestal, × 700; 11, *Q. margaretta*, stipitate-fasciculate hair seen from above, × 200; 12, *Q. minima*, sessile, fused-stellate hairs, × 250.

7 to 17 ($\overline{X}$ = 12.6) and extend 0.07–0.19 mm. ($\overline{X}$ = 0.12 mm.) (FIGURE 12). Glandular hairs are also present. Although individuals are not readily separated from *Q. virginiana* on trichome evidence, the aristate, lobed leaves and the typically shrubby habit combine to distinguish them from the live oak. The taxonomic status of this oak is in need of critical evaluation based on population studies.

Quercus montana Willdenow (*Quercus prinus* Linnaeus)

Rock chestnut oak is easily recognized by the tufted appearance of nonglandular hairs crowded into the vein axils. This pattern, although typical for many species of subgenus ERYTHROBALANUS, is unique to this species of eastern white oak. In *Quercus montana*, trichomes are attached laterally to opposing surfaces of primary veins and the midvein near their union. Density decreases sharply from the origin of vein axils to the margin, thus producing the tufted appearance. Hairs are stipitate-fasciculate, have 2 to 5 rays ($\overline{X}$ = 3.1), and are narrowly spread (0.10–0.25 mm., ($\overline{X}$ = 0.14 mm.) in spite of their length of 0.20–0.40 mm.

In addition to this trichome type, the leaf surface between primary veins contains a smaller nonglandular hair that may be erect or appressed. These hairs are solitary or are fasciculate with 2 to 5 rays ($\overline{X}$ = 2.4) that average 0.16 mm. across and vary from 0.08 to 0.25 mm. (FIGURE 13).

Quercus oglethorpensis Duncan

Oglethorpe oak, like *Quercus margaretta*, has stipitate-fasciculate, nonglandular trichomes attached to pedestals. While these species are easily separated on a variety of morphological features of the leaf (e.g., *Q. oglethorpensis* is entire, *Q. margaretta* is lobed), as well as other features, they are also distinguishable by quantitative features of their trichomes. *Quercus oglethorpensis* has 3 to 9 ray branches ($\overline{X}$ = 6.3) with a spread of 0.20–0.40 mm. ($\overline{X}$ = 0.32 mm.). Those of *Q. margaretta* are similar in ray number but average twice the spread ($\overline{X}$ = 0.64 mm.). Also, *Q. oglethorpensis* has minute, appressed, yellow, glandular hairs that are typically absent in *Q. margaretta* (FIGURE 14).

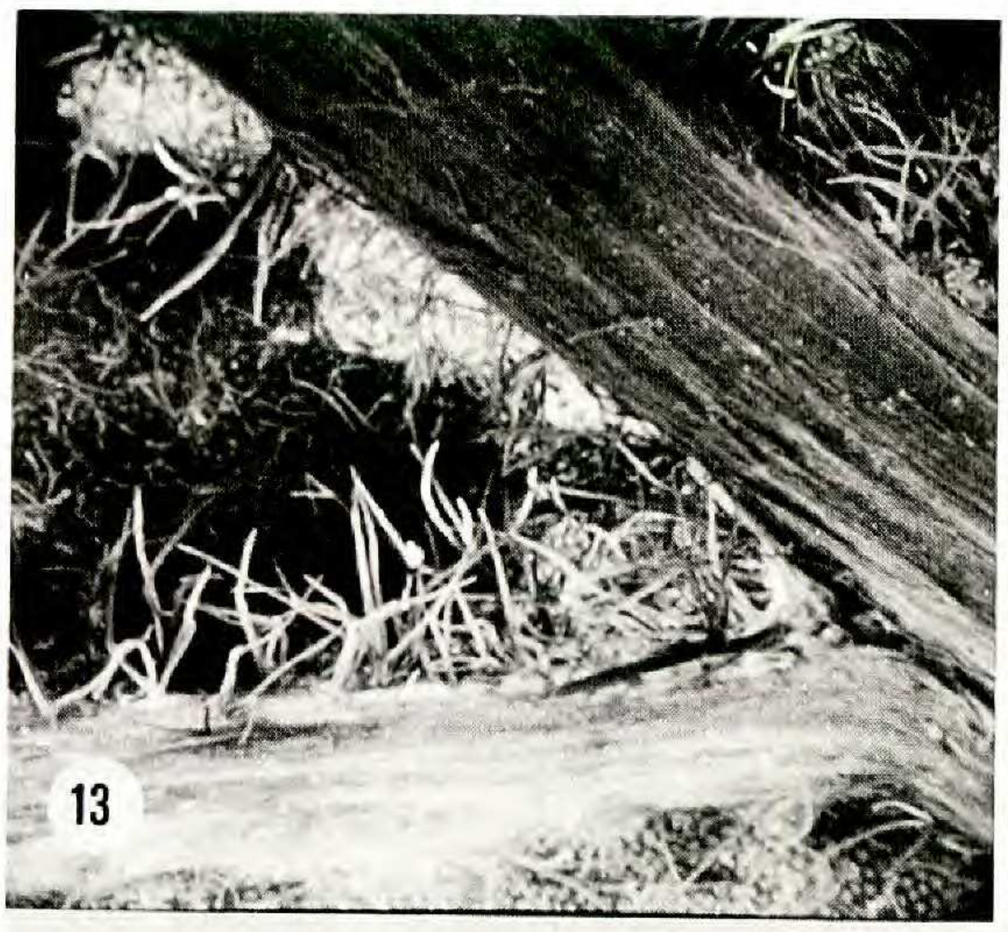
Quercus prinoides Willdenow

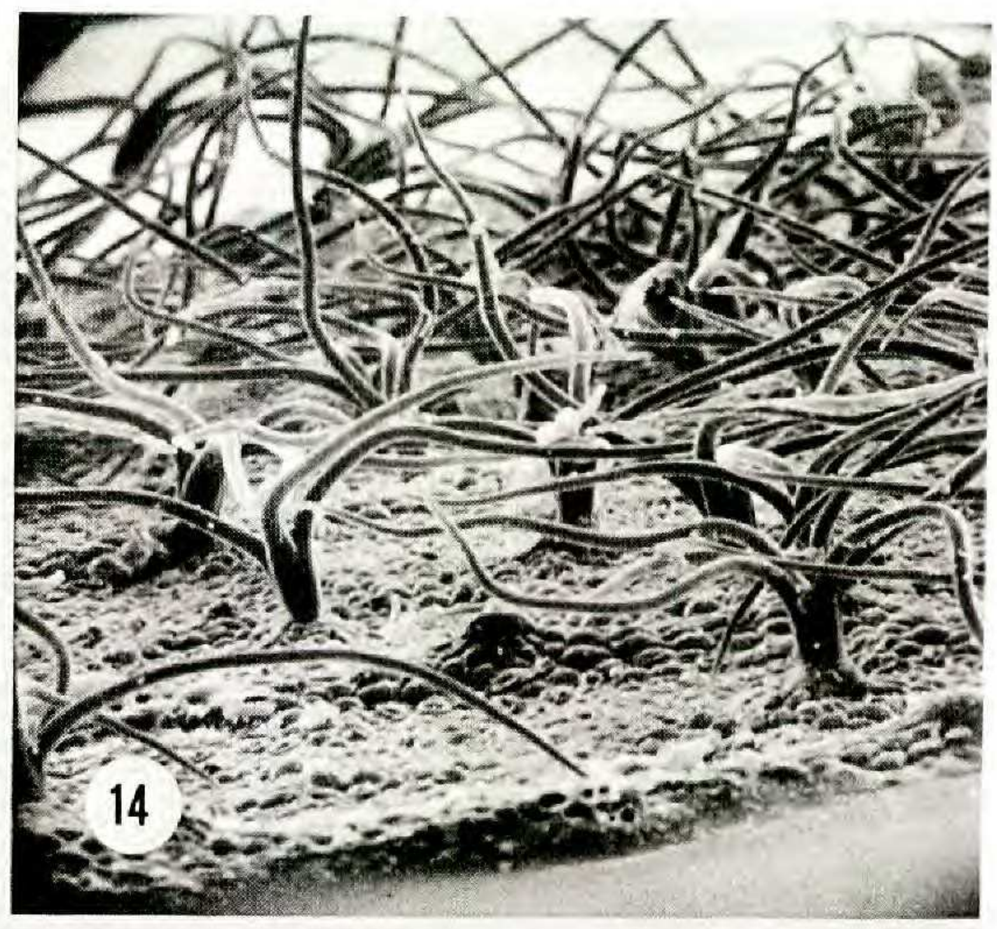
We include in this description both var. *prinoides*, the dwarf chinquapin oak, and the chinquapin oak, var. *acuminata* (Michaux) Gleason (*Quercus muehlenbergii* Engelm. of many authors), electing to follow Gleason in considering them varieties of *Q. prinoides* (FIGURE 15).

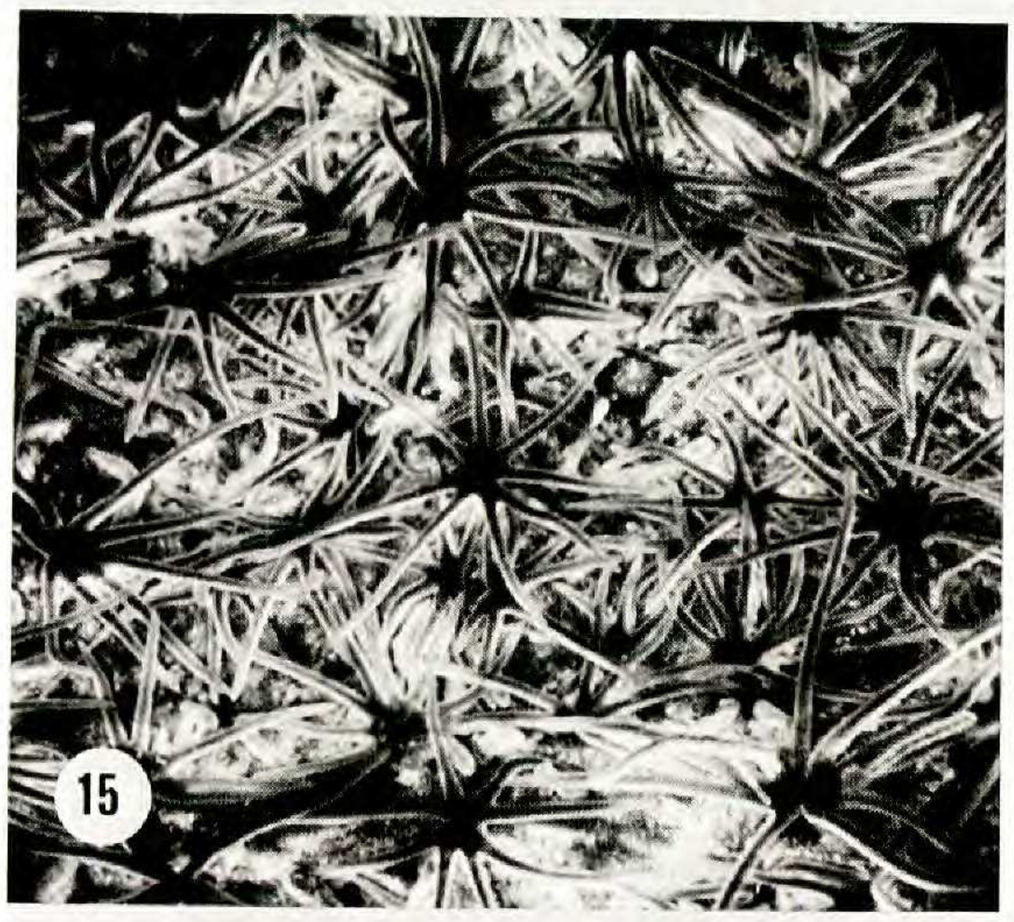
Var. prinoides

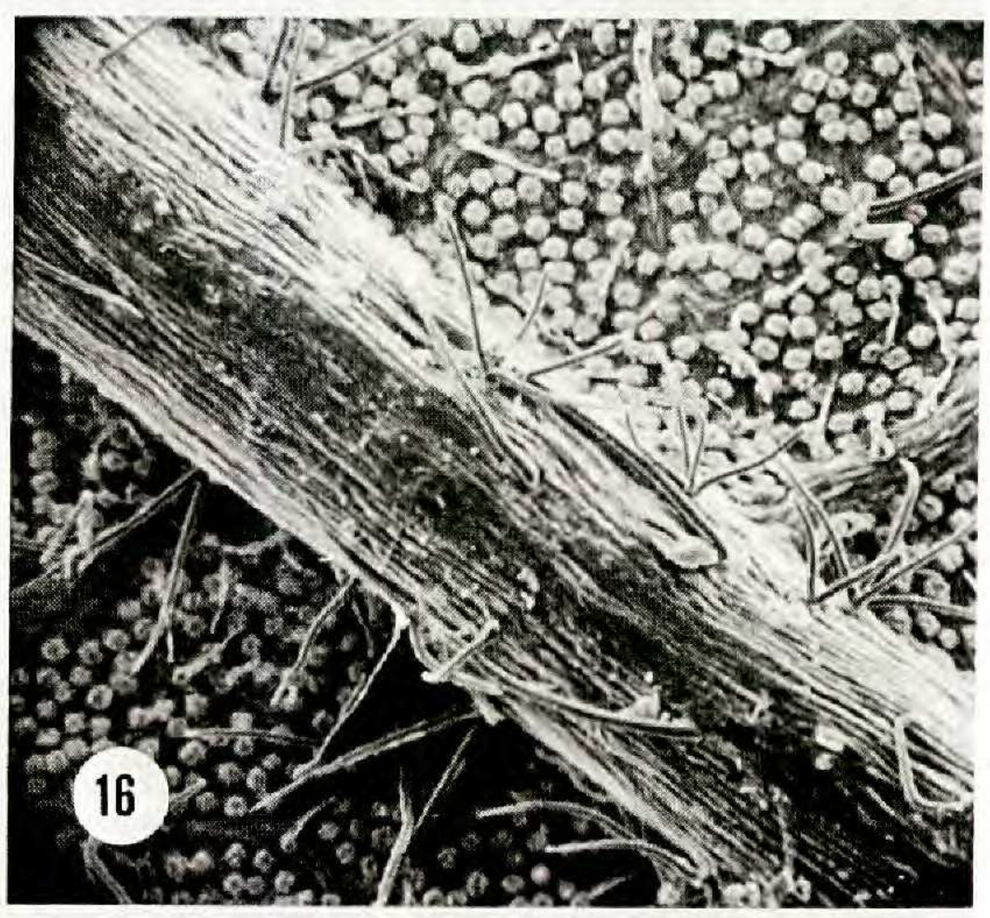
Trichomes of the dwarf chinquapin oak are stellate, appressed or looser, and whitened or with a yellowish tint; they occur on the leaf surface and lateral surfaces of the midvein and primary veins, but are conspicuously absent from the ventral surface. The hairs are small, 0.09–0.22 mm. ($\overline{X}$

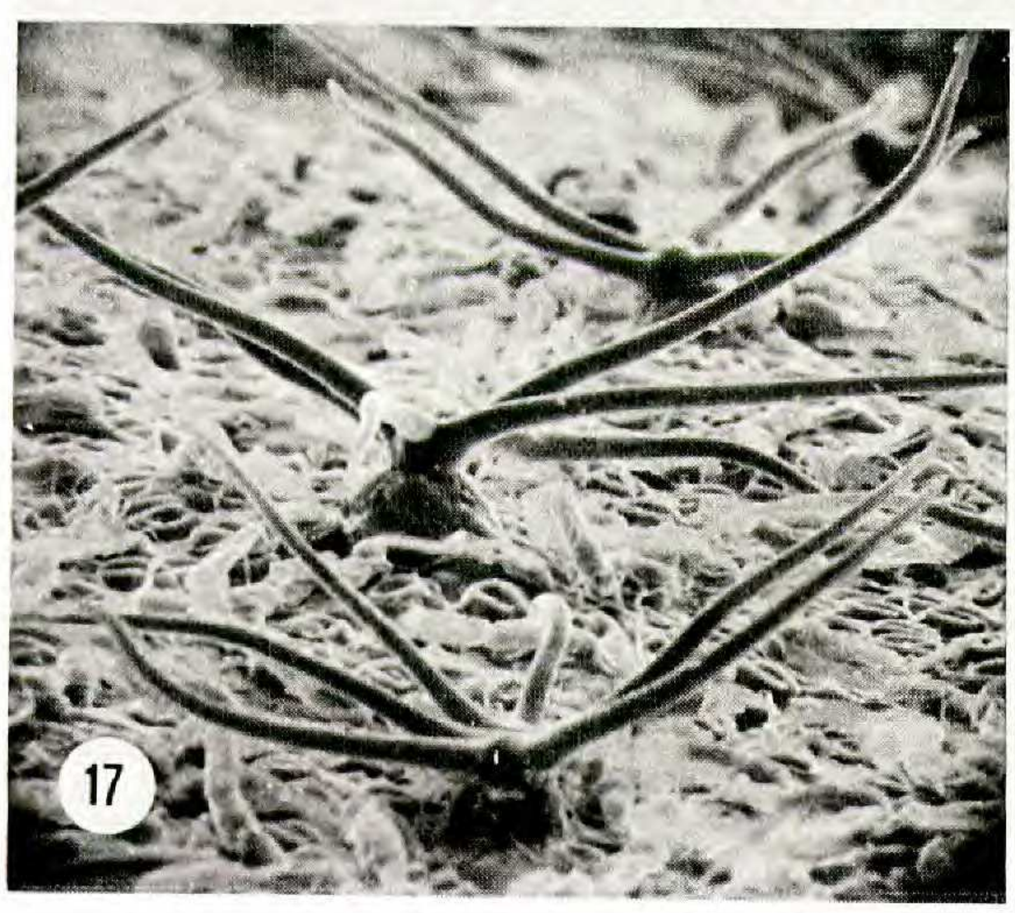
= 0.15 mm.) across, and have 6 to 16 rays per trichome ($\overline{X}$ = 10.2). Glandular hairs may or may not be present.

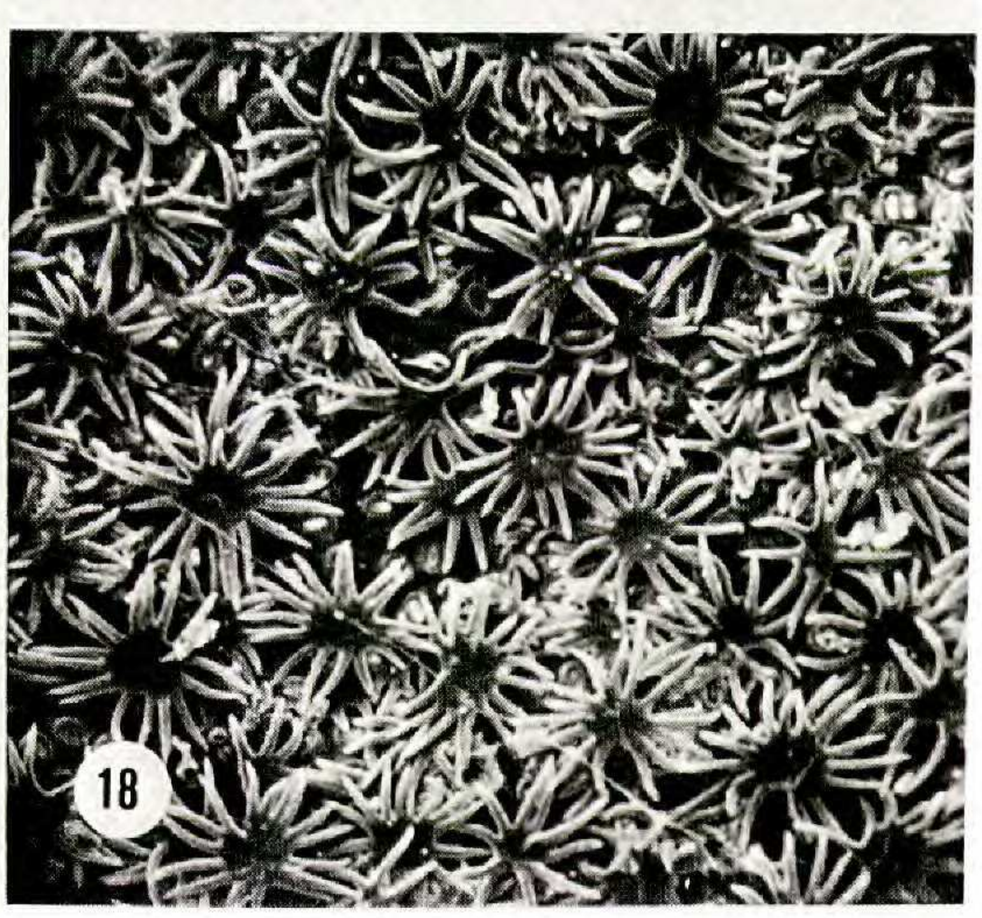












FIGURES 13–18: 13, *Quercus montana*, stipitate-fasciculate hairs (vein axils) and fasciculate hairs (lamina surface), × 50; 14, *Q. oglethorpensis*, stipitate-fasciculate hairs, × 150; 15, *Q. prinoides*, stellate hairs, × 250; 16, *Q. prinus* solitary and fasciculate hairs, × 150; 17, *Q. stellata*, fasciculate hairs, × 250 18, *Q. virginiana*, sessile, fused-stellate hairs, × 200.

Var. **acuminata** (Michaux) Gleason

Chinquapin oak trichomes do not differ in type, occurrence, color, or significantly in ray number (6 to 16, ($\overline{X}$ = 9.2) or spread (0.09–0.22 mm. ($\overline{X}$ = 0.14 mm.) from the dwarf.

Much of the material for this species was taken from field populations, but herbarium specimens were also used. In all 22 populations, a relationship to *Quercus macrocarpa* is seen in some individuals that possess a fasciculate trichome conforming in range and average for quantitative characters to the fasciculate hairs on burr oak. The smaller, stellate hairs of burr oak are nearly identical to those of *Q. prinoides* (TABLE 1). The wide leaf form of var. *acuminata* (f. *alexanderi* (Britton) Steyermark) frequently has only the larger trichomes, a condition sometimes observed in *Q. macrocarpa*.

Quercus prinus Linnaeus (*Quercus michauxii* Nuttall)

Swamp chestnut oak has the longest trichomes of all the eastern oaks. Without the aid of a microscope or hand lens, they can easily be seen arising laterally from the midvein. Nonglandular hairs are of two types: fasciculate, ranging from 0.20 to 0.45 mm. ($\overline{X}$ = 0.33 mm.) in spread, or solitary. Hairs of both types often exceed 1.0 mm. in length. The hairs are yellow or white with 2 to 4 (to 8) rays ($\overline{X}$ = 3.4). These are associated with bulbous, glandular hairs which may be erect or appressed and reddish brown. The latter occur on the leaf surface (FIGURE 16).

Quercus stellata Wangenheim

As indicated by the specific epithet, trichomes of post oak are indeed stellate in appearance. They occur on pedestals and have a spread of 0.15–0.49 mm. ($\overline{X}$ = 0.31 mm.); the rays range from 4 to 9 ($\overline{X}$ = 6.6). The yellow hairs are distributed upon the midvein and primary veins and are typically associated with small, appressed, glandular ones that are also yellow (FIGURE 17). Although the hairs diverge in nearly the same plane, they are best viewed as fasciculate types since they do show some fusion at the base.

Quercus virginiana Miller

In his 1971 treatment of the Fagaceae, Elias lists three varieties of live oak: var. *virginiana* Small, var. *fusiformis* (Small) Sargent, and var. *maritima* (Michaux) Sargent. We have treated var. *maritima* as *Q. geminata* and have discussed it separately. Described here are vars. *virginiana* and *fusiformis*. FIGURE 18 shows trichomes of *Quercus virginiana*.

Var. **virginiana**

This variety, along with var. *fusiformis* and *Quercus minima* (treated by some as *Quercus virginiana* var. *minima* Sargent), is unique in the structure of its nonglandular trichomes. The hairs are fused-stellate, appressed, and quite small. Spread varies from 0.06 to 0.18 mm. ($\overline{X}$ = 0.11 mm.).

Despite their small size, the rays are numerous. Counts ranged from 9 to 18, with 15.6 the average.

Var. fusiformis (Small) Sargent

Trichomes differ slightly from var. *virginiana*. Rays range from 12 to 24 ($X = 17.1$) but have about the same spread, 0.08–0.16 mm. ($\overline{X} = 0.12$ mm.). This variety was observed to possess yellow, appressed, glandular hairs that are typically absent in var. *virginiana*.

DISCUSSION AND CONCLUSIONS

The trichome types that offer the greatest utility for taxonomic studies of species of white oaks are nonglandular. From TABLE 1 it is evident that the fasciculate type is more prevalent than the others. When nonglandular trichomes of all types are considered, those trichomes with an even number of branches are more common than those with an odd number, and hairs with eight branches are most frequent. Glandular hairs do not lend themselves as readily for taxonomic work but are important on the basis of their presence or absence.

If their qualitative and quantitative features are combined, foliar trichomes of the eastern white oaks are separable into combinations that can be associated with established species. For a given species, variation may occur in the quantitative aspects of trichome structure over its geographic range (and probably also over its ecological amplitude), but the types present are quite uniform. For example, the fasciculate and stellate nonglandular hairs plus the red, bulbous, glandular ones provide a unique combination that is seen on leaves of *Quercus bicolor* from New York to Missouri. Spread, number of rays, and density, however, do vary within established limits, but the combination holds throughout the range. In this regard, trichomes are stable characters, perhaps more so than other qualitative features such as leaf shape.

Once the basic patterns are recognized, trichomes may be employed, with the aid of a hand lens, as useful characters in diagnostic keys for use in the field. Indeed, a key based on vegetative features in light of this evidence is planned for the eastern white oaks. Although mature leaves were used in developing the trichome descriptions, some seedlings and a few specimens with immature foliage were seen. At this time insufficient material has been examined for us to state with certainty that trichome evidence is applicable to their determination, but what we have observed encourages us to make the necessary collections in the coming year.

Trichome evidence is certainly of significance in systematic studies of the oaks and, as indicated above, has been used in combination with other characters by some investigators to establish parentage of putative hybrids. During the summer of 1974, we collected a specimen from an individual occurring in western Missouri that we suspected from leaf and fruit morphology might be a hybrid involving *Quercus stellata* and *Q. macrocarpa* (= *Q.* × *guadalupensis* Sargent). Examination of the leaves of

this individual showed it to possess nonglandular hairs of two sizes as well as glandular ones. The larger nonglandular trichomes are fasciculate and are mounted on pedestals. Their ascending rays average 6.5 per trichome and have a mean spread of 0.51 mm. The smaller nonglandular hairs are stellate with an average of 7.8 rays and a mean spread of 0.15 mm. In being attached to pedestals and having an average of 6.5 rays per hair, the fasciculate trichome resembles that of *Q. stellata*. However, the hairs are similar to those of *Q. macrocarpa* in spread and divergence. We believe the combinations of characters in these fasciculate hairs offer evidence of hybridization between the two species (FIGURE 19).

Interestingly, the stellate hairs of the suspected hybrid do not differ from those of *Quercus macrocarpa*. It is speculative at this point, but perhaps genes controlling production of different hair types are on different chromosomes, and the stellate hairs of *Q. macrocarpa* have been passed unmodified to the hybrid offspring.

The utility of trichome evidence in hybridization studies is not restricted to the eastern oaks. In a preliminary statement regarding a complex series of hybridizations among seven species of western white oaks, Tucker (1960) proposed that (among others) *Quercus gambelii* and *Q. grisea* had each crossed with *Q. muehlenbergii* (*Q. prinoides* var. *acuminata* of this

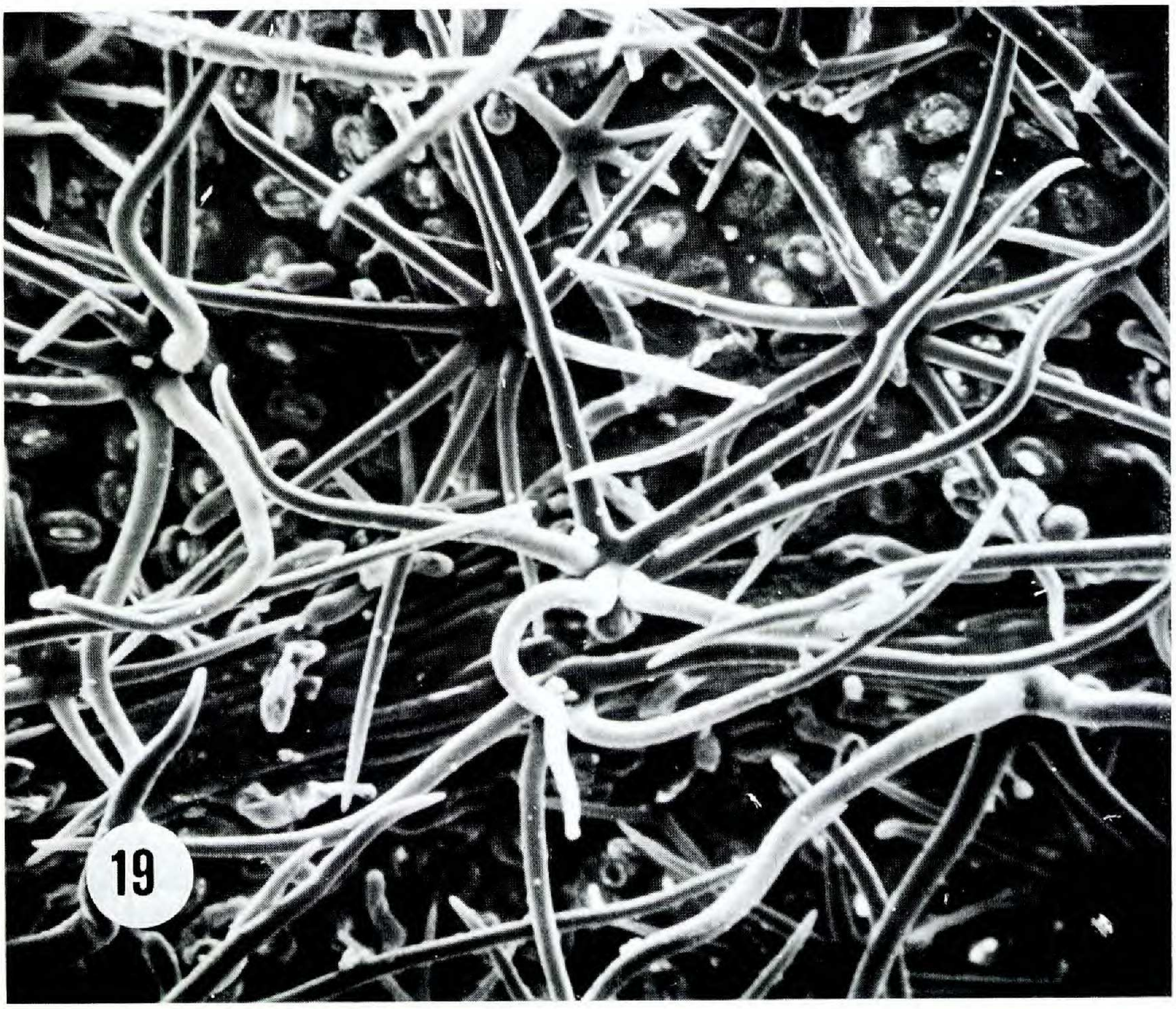


FIGURE 19: *Quercus* × *guadalupensis*, hybrid trichomes, × 250.

study). Evidence in support of these matings has not been presented by Tucker, but hybridizations involving *Q. prinoides* have been the subject of a separate study by Thomson (1978).

Plants believed to represent the crosses suggested by Tucker, and their putative parents, were collected in the Capitan Mountains of New Mexico during the summer of 1976. In both matings trichome evidence is of importance in establishing identity of the supposed parental taxa.

Quercus gambelii has nonglandular trichomes with four or fewer rays (FIGURE 20). The stellate trichomes of *Q. prinoides* (FIGURE 24) typically have eight or more rays. Both trichome types are present on leaves of *Q. gambelii* × *Q. prinoides* (FIGURE 22). *Quercus grisea* possesses nonglandular trichomes with contorted rays (FIGURE 21). The hybrid *Q. grisea* × *Q. prinoides* bears trichome types of both parents (FIGURE 23).

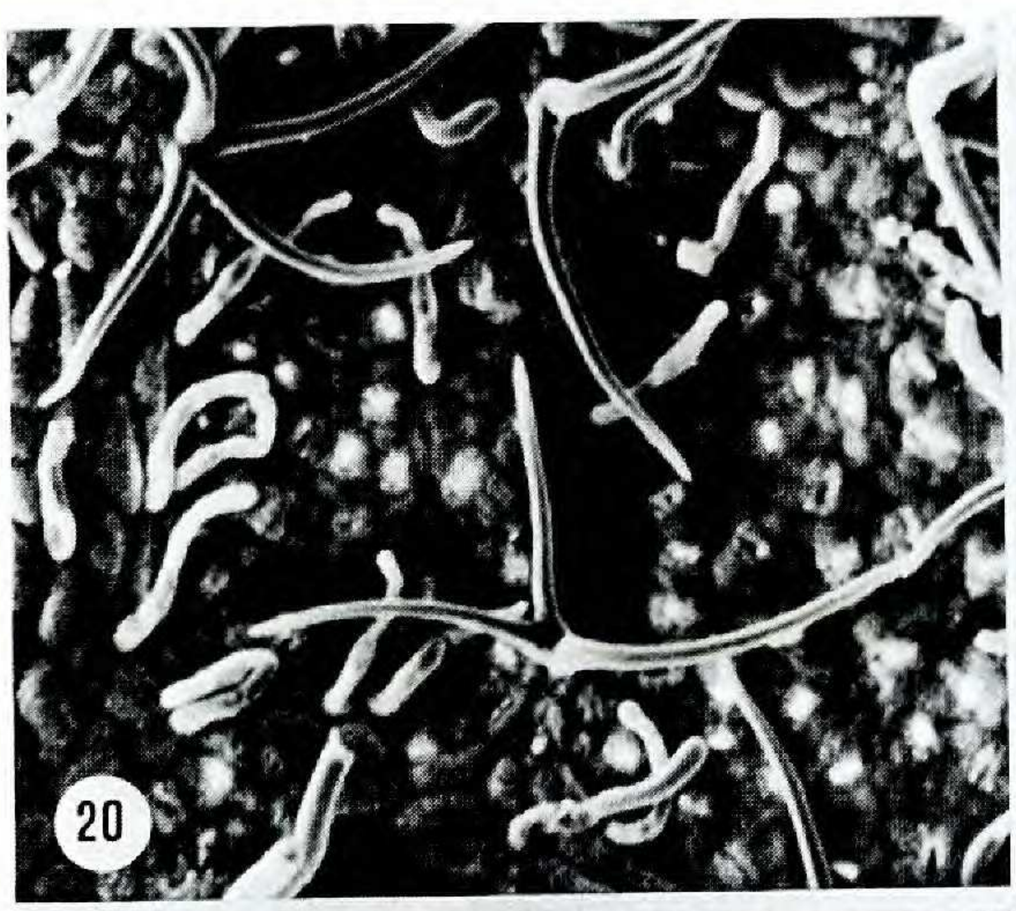
In the three examples of hybridization presented here, trichomes seem to be inherited in one of two basic ways. If the parent species have one or more trichomes of the same type (e.g., fasciculate hairs occur on the parents of *Quercus* × *guadalupensis*), hybrids demonstrate intermediacy in the quantitative features of spread and number of rays. In the second case, if parental species have trichomes of different types (e.g., fasciculate for *Q. grisea* and stellate for *Q. prinoides*), then the hybrids possess both types of hairs. In either event the trichome pattern typical of the parents is altered by the hybridization. Because the types of trichomes, their spread, and the number of rays per hair are so uniform for a species, modifications such as those described above provide strong evidence for hybridization.

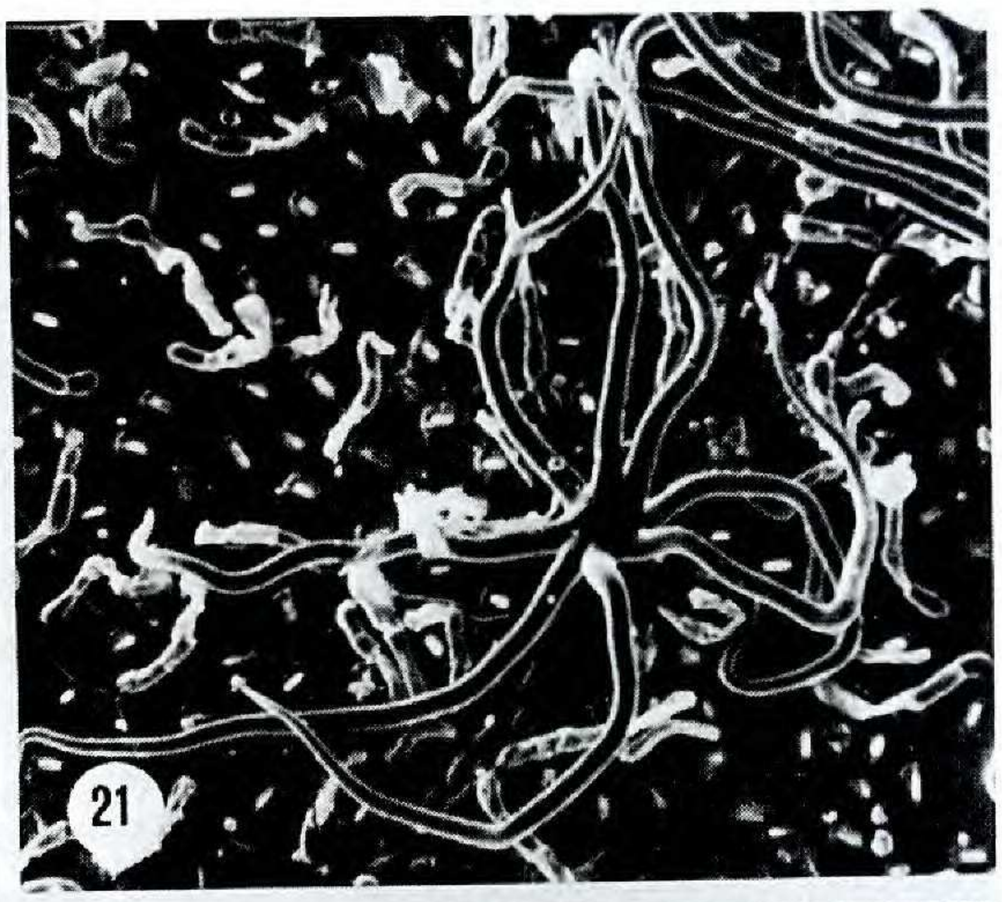
That trichome evidence may be useful in formulating phylogenetic series may be seen in its application to a lineage proposed by Duncan (1950). His phylogenetic tree for eight oaks included *Quercus oglethorpensis*, *Q. margaretta*, *Q. stellata*, and *Q. chapmanii* on one branch, and *Q. breviloba*, *Q. durandii*, *Q. austrina*, and *Q. alba* on the other. With respect to the first series, we think it is more than coincidental that trichomes of the four species are attached to pedestals, are fasciculate, have rays which vary from 4 to 9, have a mode of 8, and average 6.3, 6.7, 6.6, and 6.8, respectively. They differ in spread, decreasing nearly in accordance with the series suggested.

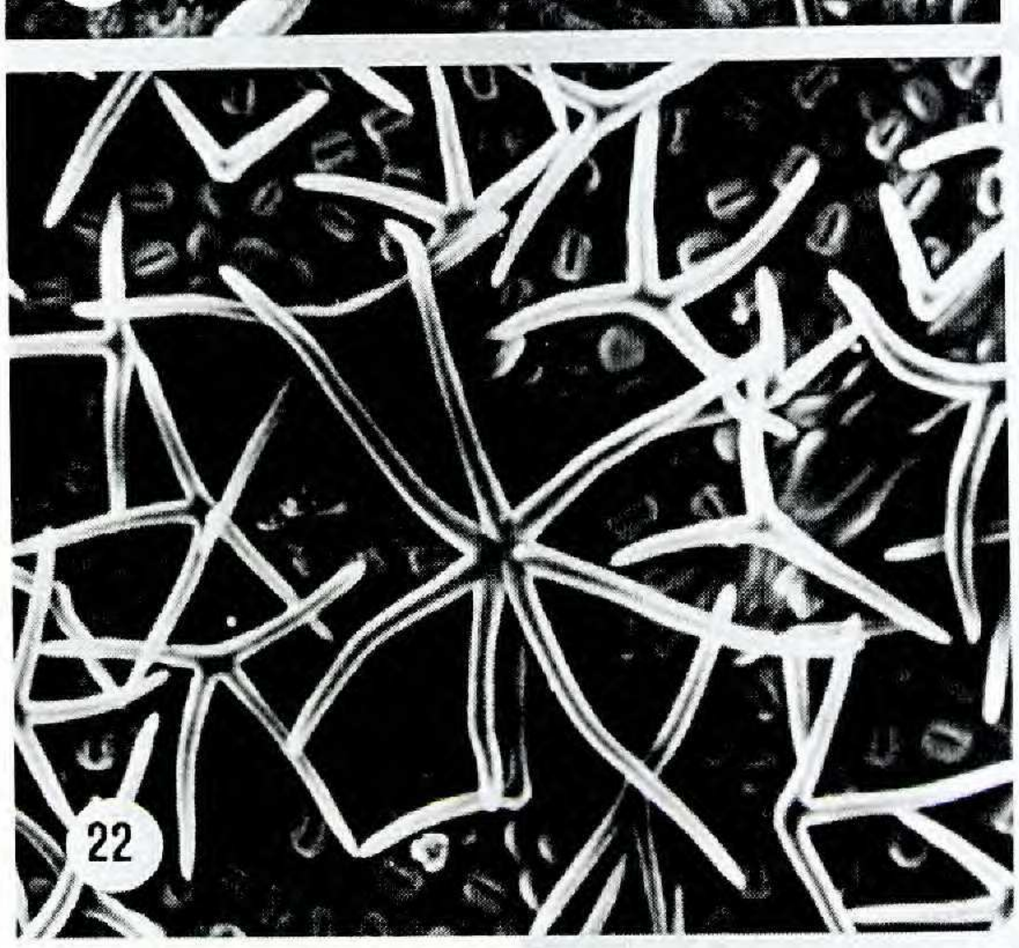
Hardin (1976) speculated that evolutionary modifications within the nonglandular class of trichomes progressed from single- to multi-celled hairs and toward vertical fusion for fascicular types. Duncan's series, which relates primitiveness to geologic distribution, portrays the phylogenetic sequence in reverse order with respect to trends in trichome structure. In his scheme *Quercus oglethorpensis* is the most primitive, but its trichomes are the advanced, stipitate-fasciculate type and lack any unicellular hairs. The most advanced, *Q. chapmanii*, has less specialized nonglandular trichomes along with simple-uniseriate ones. If fusion followed nonfused forms in the oaks, then the trends in Duncan's series are secondary.

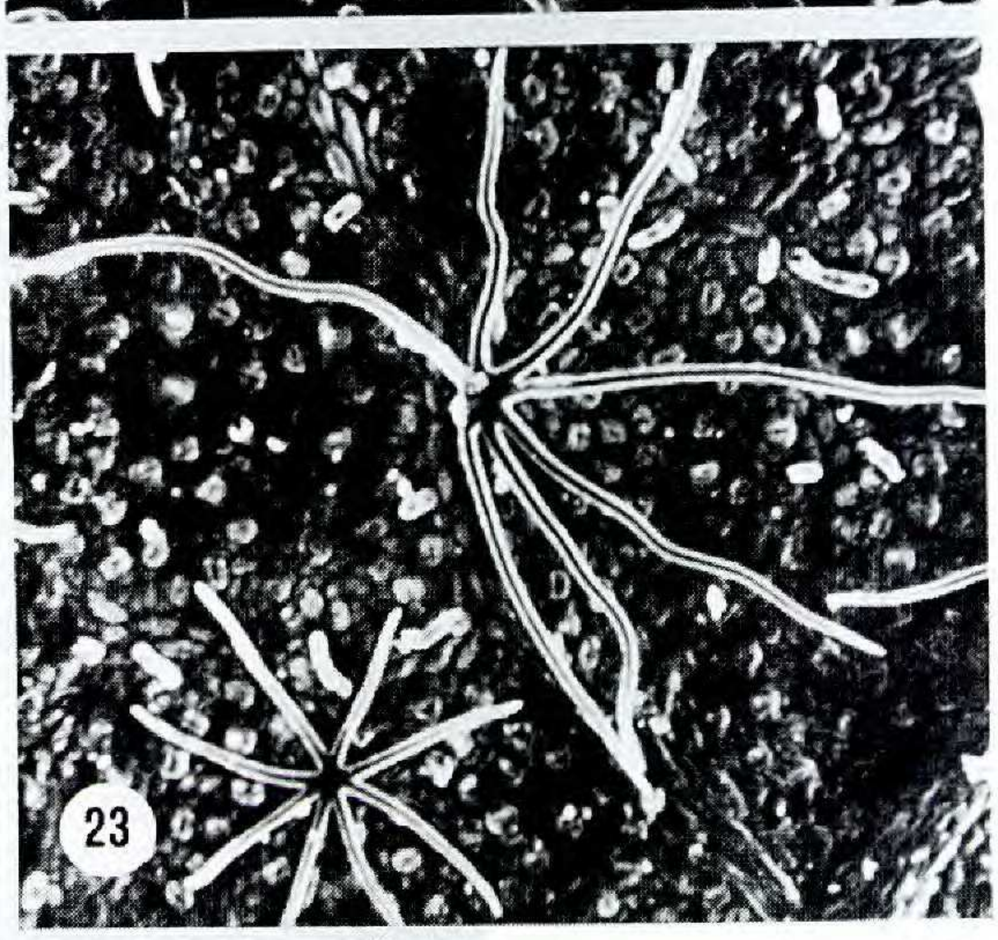
In a study of the live oak group, Muller (1963) stated that *Quercus virginiana* occurs on soils of very recent formation. It is interesting that

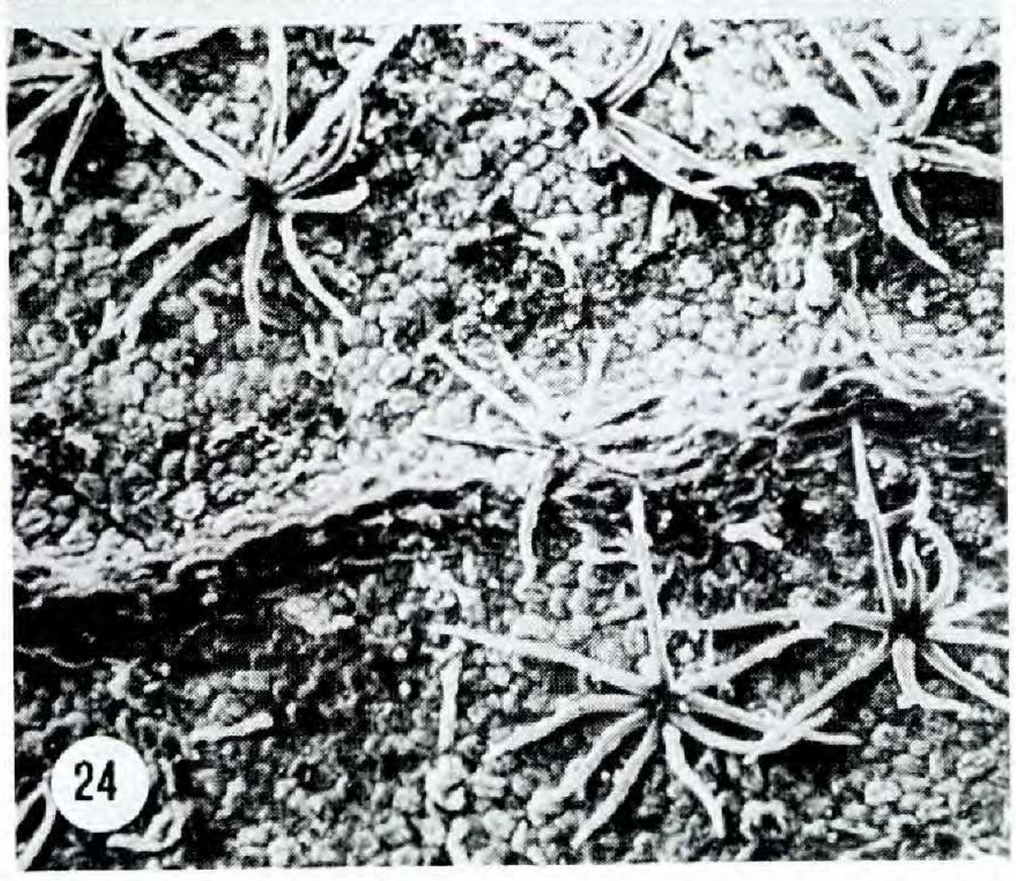
this species has one of the most advanced trichome structures, the fused-stellate type. It seems to us that trichome evidence, when combined with geologic age of the substratum, will prove to be a useful aid in interpreting phylogenetic series in this group. However, as with most morphological











FIGURES 20–24: 20, *Quercus gambelii*, fasciculate hairs, × 220; 21, *Q. grisea*, fasciculate hair, × 130; 22, *Q. gambelii* × *Q. prinoides*, hybrid trichomes, × 220; 23, *Q. grisea* × *Q. prinoides*, hybrid trichomes, × 130; 24, *Q. prinoides*, stellate hairs, × 130.

characters, without time references it is not possible to indicate for a group whether specializations are primitively simple or simple by reduction.

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